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LATE ORDOVICIAN-EARLY SILURIAN SELECTIVE EXTINCTION PATTERNS IN LAURENTIA AND THEIR RELATIONSHIP TO CLIMATE CHANGE

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INTRODUCTION

There is general agreement that the Late Ordovician mass extinction is causally related to climate change, but the precise mechanism of the relationship is not well established. A mechanistic understanding the relationship between climate change and extinction is inhibited by uncertainties about the timing, nature and magnitude of climate change and by the lack of a distinct selective extinction pattern. Here we summarize recent and ongoing work aimed at clarifying both of these uncertainties

PALEOCLIMATE RECONSTRUCTIONS

The recently developed clumped isotope proxy (Eiler, 2007) is a thermodynamically-based proxy for carbonate precipitation temperature that is independent of the isotopic composition of fluid from which the carbonate precipitated. Because it is therefore also independent of the growth and decay of continental ice sheets, it provides a means of untangling trends in local temperature from trends in global ice volume, a problem that has crippled deep-time paleoclimate reconstructions for decades. Recent application of this proxy to well-preserved Late Ordovician-Early Silurian biogenic carbonates from Anticosti Island, Quebec, Canada, and the U.S. midcontinent (Finnegan et al., 2011) suggests that the the Laurentian tropics experienced ~5° C of cooling during the Late Ordovician but that most of the cooling was restricted to the Hirnantian Stage (here we consider only the Laframboise Member of the Ellis Bay Formation to be of Hirnantian age, but our substantive conclusions would be unaffected by assigning all of the Ellis Bay Formation to the Hirnantian as advocated by some (Copper and Long, 1989; Copper, 2001; Desrochers et al., 2010; Achab et al., 2011). In contrast to the Hirnantian temperature change seen in the tropics, isotopic evidence for moderate ice sheets spans a much longer interval, from the late Katian to at least the late Rhuddanian. These data support observations from sequence stratigraphy suggesting that the growth of Gondwanan ice sheets initiated prior to Hirnantian time. Clumped isotope data also reveal a large Hirnantian peak in the $\delta^{18}O$ of seawater, suggesting that continental ice volumes at this time were very large and may have equaled or exceeded those of the last Pleistocene glacial maximum. Altogether our data supports aspects of both the protracted and short models of glaciation, with evidence for a substantial glacial maximum superimposed on a longer glacial interval that lasted ca. 10 myr. The coexistence of substantial polar ice sheets with tropical temperatures locally exceeding 35° C implies that the Late Ordovician-Early Silurian world may have exhibited steep meridional temperature gradient relative to subsequent "icehouse" modes.

EXTINCTION SELECTIVITY

Additional work on other well-preserved Late Ordovician-Early Silurian sections is required to confirm that temperature and ice volume trend from Anticosti are representative of the global tropical oceans. Such work is ongoing, but the Anticosti results provide a preliminary set of predictions about the nature and timing of environmental stresses on Laurentian marine ecosystems. Extinctions related to changes in temperature or its correlates should be limited to the Hirnantian, and those related to habitat losses and/or environmental shifts due to sea-level fall may occur throughout the later part of the Late Ordovician but should peak in the Hirnantian.

To evaluate these predictions, we combined fossil collections comprising more than 80,000 genus occurrences from the Paleobiology Database (Alroy et al., 2011) with data on the spatio-temporal fabric of the Laurentian rock record from the Macrostrat Database (Peters, 2005) to produce an integrated paleontological, environmental and stratigraphic framework for the Late Ordovician-Early Silurian of Laurentia. This framework allows us to map out patterns of faunal distribution, environmental distribution, and stratigraphic completeness for twelve late Middle Ordovician through Early Silurian time slices (see Fig. 1 for an example). Mapping genus occurrences onto sites of sedimentation allows us to determine geographic range (measured as site occupancy) for each genus in each interval. Geographic range has been shown to be one of the most consistent predictors of extinction risk both in the fossil record, and temporal changes in the buffering effect of wide geographic range on extinction risk may convey important information about extinction mechanism (Payne and Finnegan, 2007).

Because Hirnantian (or Gamachian) strata were not differentiated from Richmondian (late Katian) strata in the correlation charts on which Macrostrat is based (Childs, 1985), we have worked to refine the chronostratigraphic framework through these intervals. The refined

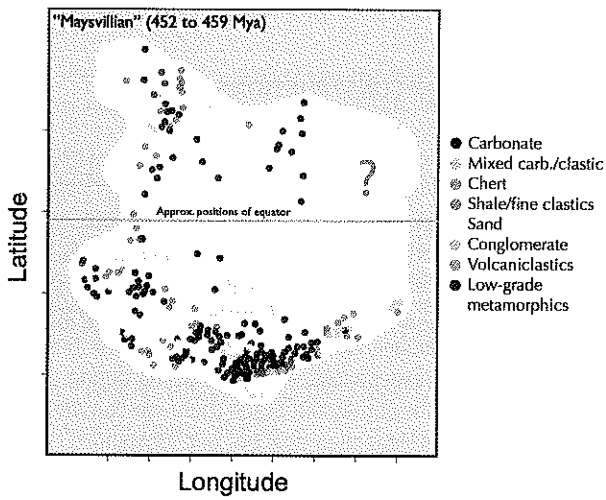

Figure 1. An example base map: distributions of sediments of definitely or likely Maysvillian (mid-late Katian) age in Laurentia. Each point represents a local stratigraphic column in the Macrostrat database, and the shading indicates lithology. Question mark indicates Greenland, which is not currently included in the Macrostrat database.

dataset confirms a very large regression in the Hirnantian, with only comparatively minor changes in continental flooding (measured by the number of sites with sedimentary rocks of a given age) through the Sandbian-Katian (Fig. 2A). As previously noted at coarser scales (Peters, 2005) trends in genus diversity bear a striking similarity to those in continental flooding (Fig. 2B).

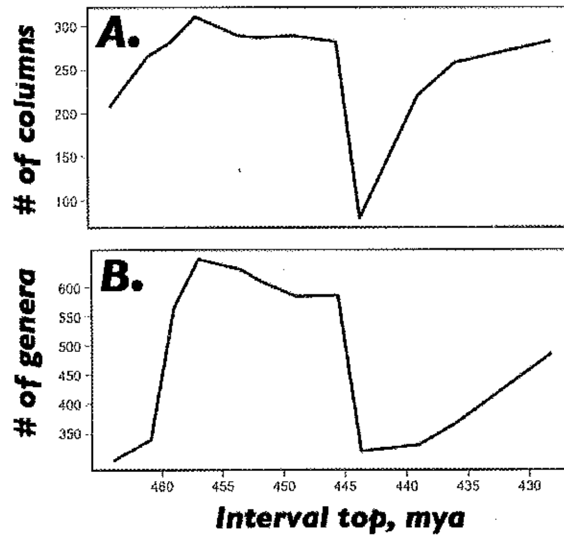

Figure 2. Time series of total number of stratigraphic columns with sediments of a given age (A) and total genus diversity (B) for Laurentia.

Although the similarity of these trends is striking, it does not necessarily prove a causal relationship -both continental flooding and extinction could be responding to a common driver -climate change- without habitat losses having any direct influence on extinction risk. We can improve on the analysis by mapping changes in continental flooding and environmental distribution onto the geographic ranges of individual taxa. Accounting for local section truncations (sedimentation at that site ceases for at least one interval) and environmental shifts (sedimentation style changes, for example from limestone to shale) permits us to calculate what proportion of each genus' range was affected by regression or environmental shifts in each time interval. Along with geographic range, these proportions can then be included as explanatory variables in a logistic regression with extinction/survival of genera as the response variable in order to determine how well habitat losses and/or environmental shifts predict not just the magnitude but the selectivity of extinction in each time interval. Within this framework we can also evaluate the explanatory power of a wide variety of other ecological variables that have been shown or suggested to be important determinants of extinction risk either during the Late Ordovician or at other time in Earth History. These include depth preference (whether the taxon tends to occur in relatively shallow or relatively deep facies), environmental preference (whether the taxon tends to occur in carbonate or clastic environments), trophic level, and life habit (benthic or not, infaunal or epifaunal).

A final variable we examined was whether or not a given genus had been sampled at high latitude (>45°) during or prior to each time interval (because the analysis is limited to Laurentia, all examined genera have at least partially tropical ranges). This variable is related to both geographic range and taxon age, but also provides information on tolerance for variation in the correlates of latitude (temperature, seasonality, etc.) -a trait that may be expected to be important during times of rapid climate change.

We used a Bayesian model averaging approach to compare all possible combinations of explanatory variables and select the set of models that explain the most variation in extinction selectivity with the fewest predictors (e.g., complex models are penalized to reflect the fact that adding new parameters always results in some improvement in model fit). Preliminary results of these analyses are summarized in Fig. 3. A variety of interesting trends are apparent. As is true for many assessments of extinction risk, geographic range (global and/or Laurentian) is an important determinant of extinction risk in most intervals, with wider-ranging genera less likely to go at extinct in any given interval. Proportional range truncation, on the the other hand, has a major influence on extinction risk only during some intervals in the Katian and, especially, at the Katian-Hirnantian boundary. Similarly, the proportion of a genus' range that experiences an environmental shift has a significant influence on extinction risk primarily in the late Katian and at the Katian-Hirnantian boundary. Another striking trend relates to the preference for carbonate or clastic environments -carbonate-preferring genera are at lower risk of extinction than clastic-preferring genera throughout much of the Late Ordovician, but this trend reverses at in the Hirnantian and remains reversed throughout much of the Early Silurian. Finally, whether or not a genus has previously been sampled at hight latitudes has a significant influence on extinction risk only at the Katian-Hirnantian boundary. This coincides with the major drop in tropical temperatures, and implies that in Laurentia extinctions driven by local climate change (as opposed to far-field eustatic effects) are largely limited to this interval. We emphasize that our conclusions are preliminary and may change as we continue to refine the chronostratigraphic, taxonomic, and paleoenvironmental framework of the dataset. However, these preliminary results are generally consistent with expectations from existing and emerging Late Ordovician-Early Silurian paleoclimatic datasets, and support a direct link between glaciation and mass extinction.

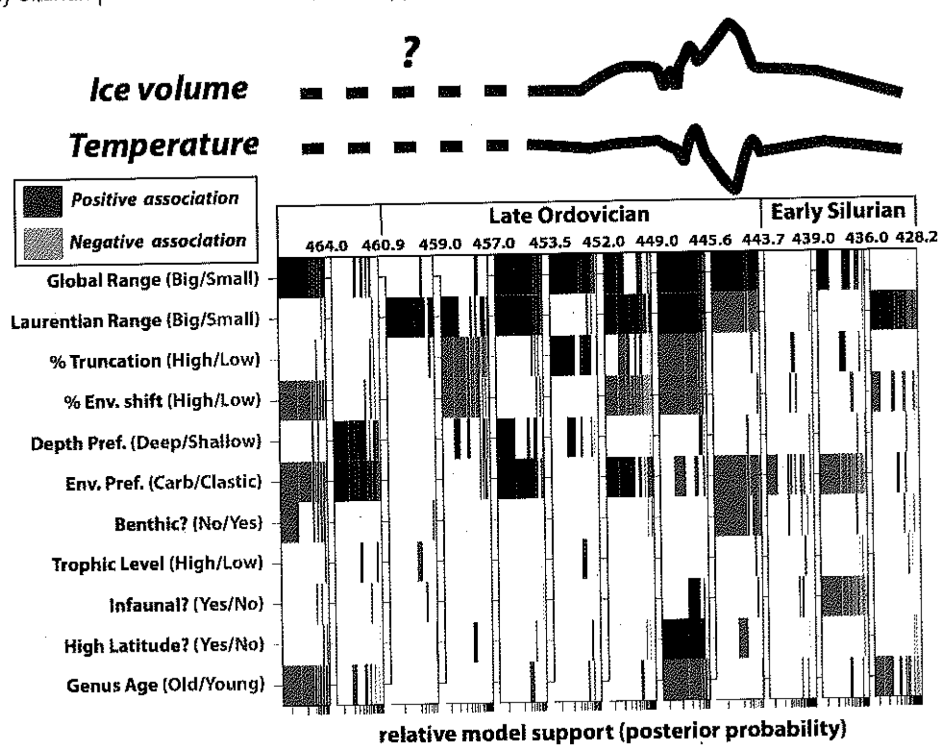

Figure 3. Results from Bayesian model averaging. All possible combinations of explanatory variables (variables indicated by text on left) are considered and the set of models that explain the most variation in extinction risk with the fewest model parameters are selected. The number of selected model is indicated by the hash marks along the x-axis for each interval; the x axis is scaled to the proportional support for each model (posterior probability) relative to the full set of most-likely models. Dark gray indicates a positive association between the predictor and extinction risk; light gray indicates a negative association, and white indicates that the variable is not included in the model in question. Ice volume and temperature trends are modified from Finnegan et al. (2011). Bottom and top ages of time intervals analyzed and indicated across below ice volume and temperature trends.

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